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THE DENTITION OF *OURAYIA*: —ITS BEARING
ON RELATIONSHIPS OF OMOMYID PROSIMIANS

ELWYN L. SIMONS

Gazin (1958) has established for the North American anaptomorph, or so-called "tarsioid" prosimian Primates two families: the Anaptomorphidae, containing seven early and middle Eocene genera; and the Omomyidae, to which eleven Eocene and one early Oligocene genera are assigned by him. It has long been recognized that members of these two families differ distinctly from the more clearly lemur-like North American prosimians of the subfamily Notharctidae, which has been suggested, originally by Leidy (1873:90) and more recently by W. K. Gregory (1921:220), as being plausibly the group from which the South American platyrrhine Primates arose. Recently, however, the candidacy of *Notharctus* and its allies for such an ancestral position has been increasingly questioned. This is because, although generalized in many ways, notharctids already show a number of features that are unlike Platyrrhini. The greater expression of the hypocone and mesostyle, together with a tendency toward doubling of the outer cusp of the fourth upper premolar — all non-platyrrhine features, but seen in the successively later species of *Notharctus*—indicate a dental pattern that was diverging from, and not approximating that which typifies the Platyrr-

rhini. Moreover, both *Notharctus* and *Suilodectes* exhibit upper third molars that, relative to the other cheek teeth, are much larger and more complex than those of the earliest known notharctine, *Pelycodus*, as well as of those of Oligocene-Recent South American Monkeys.

Some current students regard omomyid prosimians as alternative, or better, candidates for the ancestry of Ceboidea; for instance, see Gazin (1958:100). This idea appears to have had its origin in comments by J. L. Wortman (1904:242) in his imaginative but often overlooked studies on Eocene Primates at the Yale Peabody Museum. Probably the main reason the case for a possible ancestor-descendant relationship between omomyids and ceboids has not previously been considered in detail is that no really complete dentitions of members of this prosimian family have been described. Without better knowledge of the anterior dentition most of those acquainted with the problem appear to have hesitated in expressing opinions as to the phyletic relationships of this group. The completeness of the dentition in one omomyid, a specimen of *Ourayia uintensis*, described below, largely obviates this difficulty.

ACKNOWLEDGMENTS

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ABBREVIATIONS

- A.M.N.H. American Museum of Natural History, New York.
C.M. Carnegie Museum, Pittsburgh.
P.U. Princeton University, Princeton
Y.P.M. Yale Peabody Museum, New Haven

DESCRIPTION AND RELATIONSHIPS OF OURAYIA

The single species of this genus, *Ourayia uintensis*, is apparently restricted to Uinta (B) horizon of the late Eocene. It was originally described by Osborn (1895:77) as a species of *Microsyops*. Later, Osborn recognized that the assignment of this species to *Microsyops* was in error, remarking (1902:202): "Its nearer reference is either to the Anaptomorphidae or to some member of the Notharctidae." A further, but incomplete, step in the direction of a more correct taxonomic assignment for this prosimian species was made by Wortman (1904:232) who referred it to the genus *Omomyys*. However, it remained for Gazin (1958:70) to recognize that this species belongs to a distinct omomyid genus for which he coined the name *Ourayia*, after the village of Ouray to the north of the "White River pocket," Utah, from which it seems most, if not all, known specimens of this species have been recovered. Gazin (1958) noted that this genus is close to later Eocene omomyids such as *Washakius*, *Hemiacodon*, and *Stockia* and pointed out that the species differs greatly from any assigned to *Notharctus* which it resembles only in its comparatively large size. The specimens from the Princeton collections, described here, are much more complete than the American Museum materials available to Gazin and further serve to emphasize the distinctness of the dentition of *Ourayia* from that of any notharctid. In view of the completeness of the specimen P.U. 16431 it is now possible to define much more adequately the structure and relationships of this primitive prosimian.

Order PRIMATES Linnaeus 1758

Suborder PROSIMII Illiger 1811

? Infraorder LEMNIFORMES Gregory 1915

Family Omomyidae Gazin 1958

Subfamily Omomyinae Wortman 1904

OURAYIA Gazin, 1958

Type species: *Ourayia uintensis* (Osborn), 1895.

Included species: *Ourayia uintensis*.

Distribution: Late Eocene, Uintan stage; White River pocket, Uinta Basin, Uintah County, Utah.

Generic distinctions: In addition too having lower and more anteroposteriorly elongated trigonids and comparatively larger talonid basins than in *Hemiacodon*, as mentioned by Gazin (1958:71) for *Ourayia*, the hypoconid is less anteroposteriorly compressed than in *Hemiacodon* and does not project as far laterally from the main body of M_1 as it does in *Stockia* and *Hemiacodon*. M_{1-2} hypoconulids are not distinctly set off as in *Hemiacodon* and *Washakius*. Resembles *Hemiacodon* and differs from *Washakius* in lacking molar metastylids. In *Ourayia* the apices of molar paraconids are situated somewhat more internally than in *Stockia* and M_3 hypoconulids are comparatively smaller than in *Hemiacodon* and *Washakius*. Second and third molars above and below are larger compared to first molars than in *Washakius* and *Hemiacodon*. *Ourayia* agrees with species of these two genera in having crenulate tooth surfaces, but unlike *Washakius* has only a single metaconule. Differs from *Hemiacodon* in having a much less sharply broken crest between para- and metacones and no appreciable development of P^1 parastylar cuspule. Anterolingual cingular region of M^{1-2} shows a pericone variably present as is the case also in *Hemiacodon* and *Omomys* among omomyids and in the living platyrrhine *Samiri sciurca*.

Discussion: One difference between *Ourayia* and *Hemiacodon*, noted by Gazin (1958:71), that the M_2 paraconid of the former is nearly obscured in the anterior trigonid crest, is now seen to be a feature of the type specimen alone. The M_2 paraconid on both sides in P.U. 11236 and P.U. 16431 shows distinctly. This difference, together with slightly smaller size and less oval M_2 outline in the latter two specimens might suggest a species distinction for the Princeton materials were they not from the same horizon and area as the type. Gazin pointed out that the lower dentition of this primate does not resemble *Notharctus*. This conclusion is amply confirmed in the upper dentition of *Ourayia* where, apart from basic differences in cheek tooth crown patterns, the upper incisors are seen to be

comparatively huge and the canine much reduced. These features, together with the loss of $P_{1/1}^1$, are in marked contrast to the situation in notharectines which have small upper incisors and long canines. The difference here is of the same order of magnitude as that separating Malagasy lemur from loris dental patterns and amply justifies reference of *Ourayia* and *Notharectus* to different families.

As regards the phyletic position of *Ourayia* among omomyids I suspect that the genus may have been derived directly from *Hemiacodon*, particularly since the M_2 paraconid is not as unlike that of *Hemiacodon* as was supposed from the type specimen alone.

Possible relationships with the early Oligocene *Macrotarsius montanus* are less certain, but direct derivation of this species from *Ourayia* is not out of the question. Crenulations of the enamel resembling those of both *Hemiacodon* and *Ourayia*, although less pronounced, are evident in the talonid basins of the Oligocene form. Paraconids are situated slightly more laterally than in species of the latter two genera, but this difference need not rule out a close relationship between them and *Macrotarsius*. Present knowledge of the relative size, number and positioning of the anterior lower teeth in several omomyid genera, *Omomys*, *Washakius*, *Chlororhysis*, *Hemiacodon*, and *Ourayia* strongly suggests that Clark (1941:562) was correct in interpreting the lower dental formula in this Oligocene omomyid as 2.1.3.3, the typical formula for the group. If P_1 is lost and P_2 single-rooted as in other Omomyidae, then the small anteriormost remaining tooth in *Macrotarsius* must be the base of a reduced canine (see fig. 1). This canine, however, is not less prominent than in any other omomyid as Clark suggested, although the lateral incisors do appear to reach an extreme of reduction, judging from the alveolus. In *Ourayia*, moreover, the lower incisors are more procumbent. To the extent that the species of *Hemiacodon*, *Ourayia*, and *Macrotarsius* are in, or close to, a single progressing phylum, the suggested trends, apart from size increase, were toward deepening and shortening of the ramus mandibuli, together with a size reduction and more vertical implacement of the lower incisors. Perhaps the latter changes are to be correlated

with increasing use of the hands in feeding and with facial foreshortening.

OURAYIA UINTENSIS (Osborn), 1895

Figures 1, 2, 3.

Microsyops uintensis Osborn 1895, Bull. Amer. Mus. Nat. Hist. No. 7, pp. 77, fig. 1.

Omomys uintensis Wortman 1904, Amer. Jour. Sci. 4th Ser., Vol. 17, pp. 134, 135.

Ourayia uintensis Gazin, 1958, Smithsonian Misc. Coll. Vol. 136, No. 1, pp. 70-72, pl. 13, fig. 8.

Type of genotypic species: A.M.N.H. No. 1899; left mandibular ramus with P_3 - M_2 .

Type locality: Late Eocene, Uinta (B), White River, Utah.

Hyopdigm: Type and A.M.N.H. 1900, mandibular fragment with right M_1 ; P.U. 11236, left and right mandibular rami with left P_3 - M_3 (lacking trigonid of M_2 , alveoli of P_1 ; right P_1 - M_3 (trigon of M_1 missing), alveoli of I_2 - P_3 ; P.U. 11288, edentulous right mandibular ramus; P.U. 16431, maxillae with upper dentition excepting left P^2 , mandibular fragments with left I_1 , P_{3-1} , damaged M_1 , M_2 - M_3 ; right I_1 , damaged P_3 , M_1 - M_2 , trigonid of M_3 .

Horizon and locality: Lower Uinta [B], upper Eocene, White River Pocket, Utah. P.U. 16413, Section 2, T. 9 S., R. 20 E. Uintah County, Utah; P.U. 11236, 11288 Uinta [B], Kennedy's Hole, White River, Utah.

Specific diagnosis and description:¹A moderate sized prosimian; comparable parts approximately within the size range of the living *Perodicticus potto*. Dental formula 2.1.3.3; I_2 spatulate, and somewhat procumbent,

2.1.3.3

posteriorly with median vertical ridge and basal cingulum rising internally halfway toward crown; I_3 smaller than I_2 (alveolus); \bar{C} probably smaller than I_2 (root), no diastema; P_2 single-rooted; P_3 with internal cingulum lacking on P_4 ; P_{3-4} of equal height, paraconid, metaconid, and external cingulum present in P_4 , -lacking in P_3 , heel of P_{3-4} with single cusp situated laterally. Surfaces of cheek teeth, particularly, bearing wrinkled or crenulate patterns. M_2 slightly larger and more oval in outline than M_1 . Molar paraconids distinct (except in M_2 of type), situated only slightly less laterally than metaconids and connected with protoconids by an arcuate crest. Hypoconulids not sharply set off on M_{1-2} . M_3 hypoconulid not as

¹ I fail to grasp fully the logic behind the increasingly popular practice of neglecting to distinguish between generic and specific diagnoses in treatments of monospecific genera. Generic characters, in this case, are those features which prevent reference of such species to other genera; the specific, those attributes which, combined, characterize a given, and no other, species. The two suites of features are not indistinguishable, although I suspect that the failure to see that they are not may be one prime contributor to the production of unnecessary or invalid genera.

large as in most earlier omomyids. Upper incisors large, I^{2-3} sub-equal in size, spatulate; upper canine reduced, premolariform, smaller than P^2 ; P^2 small, lacking lingual cusp; P^{3-4} with single inner and outer cusps. M^{1-3} with para- and metaconules, varying expression of cuspules on lingual protocone cingulum in positions of hypocone and pericone, pronounced labial cingula with cuspule not seen in *Hemiacodon* in position of mesostyle.

Discussion: *Ourayia uintensis* is of greater size than are other known omomyids except for the considerably younger species *Macrotarsius montanus* of Chadronian age, which is about ten percent larger in comparable parts. Among omomyids earlier or contemporary with *Ourayia*, *Hemiacodon gracilis* most nearly rivals it in size, being about eighty-five percent as large in most measurements. The remote possibility that canines were lost in *O. uintensis* and that there were actually four premolars above and below in this species has been considered but rejected. In spite of its premolariform appearance, the upper canine apex is directed forward while that of P^2 has a distinct backward tilt which can hardly be due to crushing. Moreover, occlusion of the teeth in P.U. 16431 shows that the lower canine (which has a larger root than the teeth adjacent to it) lies in front of the upper canine, as would be expected.

The maxillae of P.U. 16431 are crushed, but some features of interest are still to be observed (see fig. 2). Much of the premaxilla of the right side is preserved, and a wavy suture just in front of the canine and arching backward is indicated on both sides. Both narial margins of the premaxillae are evident anteriorly. The thin, fairly long right nasal has dropped down between the premaxillae. In the orbital region the jugal is missing and the orbital border of the right maxilla much eroded, so that it is not possible to determine whether the malar contacted the lachrymal. However, it is difficult to avoid the conclusion that the orbit was quite large relative to the size of the rostrum. This possibility is also indicated by a specimen of *Hemiacodon* figured by Gazin (1958: pl. 4, fig. 4) in which the supraorbital border of both orbits is preserved. Since this specimen and P.U. 16431 are the only individuals of any species of omomyid primate which preserve part of the skull other than maxillae or dentaries, they deserve special comment. It appears that in *Ourayia* the depth of the rostrum

above the canine was greater than the horizontal distance from the narial to orbital borders, so that this primate shows the progressive feature of being comparatively short snouted, evidently much more so than in *Smilodectes* or *Notharctus*. On the other hand, this "advanced" omomyid feature is balanced by the presence of a metopic suture between the frontals in *Hemiaecodon* figured by Gazin as is generally the case in "primitive" or non-tarsioid prosimians.

The reduced upper canine of *O. uintensis*, taken together with possession of a lower canine root that is hardly larger than P_2 in cross-sectional area, indicates a small, premolariform lower canine. Both Matthew and Granger (1915: fig. 24) and Gazin (1958: pl. 8) illustrated specimens of the closely related *Hemiaecodon gracilis* which preserve broken lower canines that are indeterminate as to the height of this tooth. A specimen of *H. gracilis* recently located in the Yale collections, Y.P.M. 16253 from Henry's Fork, Wyoming, shows that the entire tooth was extremely premolariform and only barely higher than P_2 (see fig. 1). In view of an overall similarity in general size and proportions of the other teeth between *O. uintensis* and *H. gracilis*, the reduced upper canine of the former almost certainly opposed a premolariform tooth below. In earlier omomyids, *Omomys* and *Chlororhysis*, the lower canine is relatively larger (fig. 1). Such canine reduction in the later omomyids practically eliminates them from consideration as being ancestors of any Ceboidea.

Although *O. uintensis* may be derived from *H. gracilis*, reference of the former species to the genus *Hemiaecodon* seems out of the question. The primary distinctions between these two genera have been cited in the diagnosis given above (page 4), and they are considerably greater than those which have been proposed as separating the genera *Omomys*, *Loxocina*, and *Chlororhysis*. No doubt, known omomyid species could be lumped under fewer genera, but in the fragmentary state of present knowledge concerning them, limited almost entirely to dentitions, this would serve no useful purpose and in any event cannot be attempted here.

Curiously, wear on M_1^{-1} of *O. uintensis*, P.U. 16431, is distinctly less than on M_2^{-2} . That this could be due to misinter-

pretation of the dental formula, with molariform $P_{\frac{4}{4}}$ and loss of one of the molars seems impossible, particularly because in the closely related *H. gracilis* the normal sequence of molar wear can be established for numerous specimens.

MEASUREMENTS IN MILLIMETERS OF *OURAYIA UINTENSIS*
LOWER DENTITION

	P.U. No. 16431	P.U. No. 11236	A.M.N.H. 1899
Length $I_2 - M_3$	27.6
Length $P_3 - M_3$	18.0	18.8
Length $P_3 - M_2$	13.0	14.6	15.0
Depth of jaw below M_1	6.2	6.8	7.6
Transverse diameters: I_2	2.0	1.9
I_3
C
P_2	1.1(?)
P_3	2.0	2.3	2.3
P_4	2.7	2.5	2.6
M_1 (trigonid)	3.0	2.8	2.9
M_2	3.1	3.1	3.4
M_3	2.9	3.0
M_1 (talonid)	3.5	3.3	3.6
M_2	3.6	3.3	3.8
M_3	3.2	3.0
Anteroposterior diameters:			
I_2	2.3	2.1
I_3
P_2	1.8(?)
P_3	2.9	3.1	3.2
P_4	3.1	3.7	3.7
M_1	4.0	4.2	4.6
M_2	4.2	4.2	4.5
M_3	5.2	4.6

UPPER DENTITION

	P.U. No. 16431
Length I ² — M ³	28.9
Length P ³ — M ³	17.5
Transverse diameters: I ²	1.7
I ²	1.7
C	1.4
P ²	1.4
P ³	3.1
P ⁴	3.8
M ¹	4.8
M ²	5.2
M ³	4.8

Anteroposterior diameters:

I ²	3.4
I ³	3.1
C	2.2
P ²	2.3
P ³	3.1
P ⁴	3.0
M ¹	3.8
M ²	4.1
M ³	3.8

Measurements for a possibly associated right P₂ of P.U. 16431 have been given above. Although there is no definite contact between this tooth and the right mandibular fragment, it is the proper size and shape for an omomyid P₂, judging from morphology of P₂ in *Omomys* and *Hemiacodon*.

RELATIONSHIPS OF THE OMOMYIDAE

The hypothesis that omomyid prosimians may be near the ancestry of the platyrrhine monkeys is based on several points of direct and indirect evidence, most of which are rather

equivocal, as is often the case with such phyletic conjectures. For those who do not favor a notharctid derivation for platyrrhines these small Primates remain as the only other group now known in North America which contains members that are early and generalized enough to admit of such a relationship. Other early Cenozoic families of North American Primates including Plesiadapidae, Carpolestidae, Anaptomorphidae, Phenacolemuridae, and Paromomyidae (if the latter two are regarded as distinct) exhibit extreme tooth specialization or reduction which entirely eliminates their known members from any ancestral relation to the South American Monkeys. It is clear, however, that if the dental form and arrangement of *Ouvayia uintensis* was at all typical of the later Omomyidae as a whole, it would require a reversal of the trend toward reduction of the canines, seen in this species in order to reach the condition typical of the ceboid monkeys. Such a possibility seems at best rather unlikely.

The question of the ancestry of the platyrrhine monkeys bears rather crucially on the interpretation of a number of more general assumptions inherent to the currently accepted higher categories of Primates, particularly the concept of the suborder Anthropoidea, as well as to the widely accepted succession of grades, from lemuroid to tarsiod, to monkey and etc., through which the ancestors of man and the other Higher Primates are commonly supposed to have passed. Perhaps the problem is largely semantic, resulting from the all too human tendency to superimpose an idealistically subdivided terminology on what are actually continua of evolving lineages. Nevertheless, most of the various named higher categories of Primates have been, and presumably will continue to be, useful in talking about evolutionary relationships within the order. One possible reaction might be to suspend judgement or discussion of relationships between early and late Cenozoic Primates in view of the partial and fragmentary evidence now available, but within the framework that has been set up by previous research it seems advisable to follow out some earlier suggestions to their logical conclusion. For instance, if platyrrhine monkeys were actually derived from anything like the *Notharctus* group or even from the omomyid

prosimians, it is difficult to see how they could have passed through a grade of organization that need be qualified as tarsioid. If either of these groups are actually ancestral to the South American Monkeys, but not to the Old World Higher Primates, then it is also necessary to conclude that those features which are shared by Old and New World Higher Primates are the result of parallel evolution and that these two groups were independently derived from the Prosimii.

In the latter case the taxon Anthropoidea consists of a grade in the sense of Huxley (1958) rather than a clade, in which the common ancestor of subsequent derivative stocks shares something of the definition which justifies the association of such subsequent groups within a single taxon. If Catarhini and Platyrrhini were derived from independent stocks of Prosimii, then Anthropoidea have a polyphyletic origin, even if such stocks belonged to the same major division of prosimians.

When considering the various alternatives for the derivation of the Platyrrhini it may be noted that latest species of the genus *Notharctus*, and of *Smilodectes* as well, are rather large prosimians, having approximately the body size range seen in species of the living Malagasy genus *Lemur* or in the domestic cat. It seems implausible, although not impossible, that forms such as the pigmy marmoset could have descended from ancestors of the size range of known notharetids. The smallest notharetids, species of the early Eocene genus *Pelycodus*, in comparable parts, have about twice the linear dimensions of the smaller species of *Callithrix* and are even larger compared to *Cebuella*, should the latter genus be sustained as distinct from *Callithrix* [*Hapale*]. Inasmuch as known species of *Pelycodus* give every evidence of being close to the origin of the taxon Notharctidae, there is little reason to posit that there ever were unknown smaller members of this subfamily from which marmosets such as *Cebuella* might more plausibly have been derived without marked size decrease at some intermediate period. One is therefore faced with the supposition that, if Notharctidae are in or near the ancestry of platyrrhines, marmosets have undergone a size reduction since their initial differentiation. This view has sometimes been put forward, but to date there is no paleontological evidence for it.

In conclusion, it is possible to say that in spite of the fact that late Eocene and Oligocene omomyids were specializing along distinct lines of their own, not foreshadowing Platyrrhini, it seems probable that *Omomyys* and its immediate forebears are the most likely early Cenozoic prosimians to have a direct relationship to the rise of the South American Monkeys. Among principal evidences supporting this view are the observations that *Omomyys*, or one or more forms allied to it, was smaller than any known ceboids, had suitably unspecialized molar crown patterns together with small third molars, shared with some ceboids the otherwise nearly unique possession of a pericone cusp, and belongs to a group showing trends away from the primitive prosimian condition toward foreshortening of the rostrum, orbital enlargement, and vertical incisor emplacement. Moreover, Omomyidae are the only known family of ancient and undoubted Primates now known which possessed exactly the same dental formula as do the living Cebidae. Nevertheless, only in earliest omomyids are relative sizes of respective tooth types reasonably satisfactory for derivation of the tooth morphology characteristic of Oligocene-Recent South American Monkeys.

Figure 1.

Diagrammatic reconstructions of a sequence of representative omomyid species, approx. x 3. Dotted outlines hypothetical.

These species may not represent a single phylum, but each is typical of the successive Epoch substage to which it belongs. Specimens on which this chart is based are as follows: *Macrotarsius montanus* (type) C. M. 9592 (reversed); *Ourayia nintensis*, P.U. 16431 (P_1 and M_1 reversed from right ramus); *Hemiacodon gracilis* (composite), part A—A.M.N.H. 12037, part B—Y.P.M. 16253, part C—Y.P.M. 12987-1; *Omomys carteri* (composite), part A—A.M.N.H. 12600, part B—Y.P.M. 16287 (reversed), part C—Y.P.M. 13219-2 (reversed).

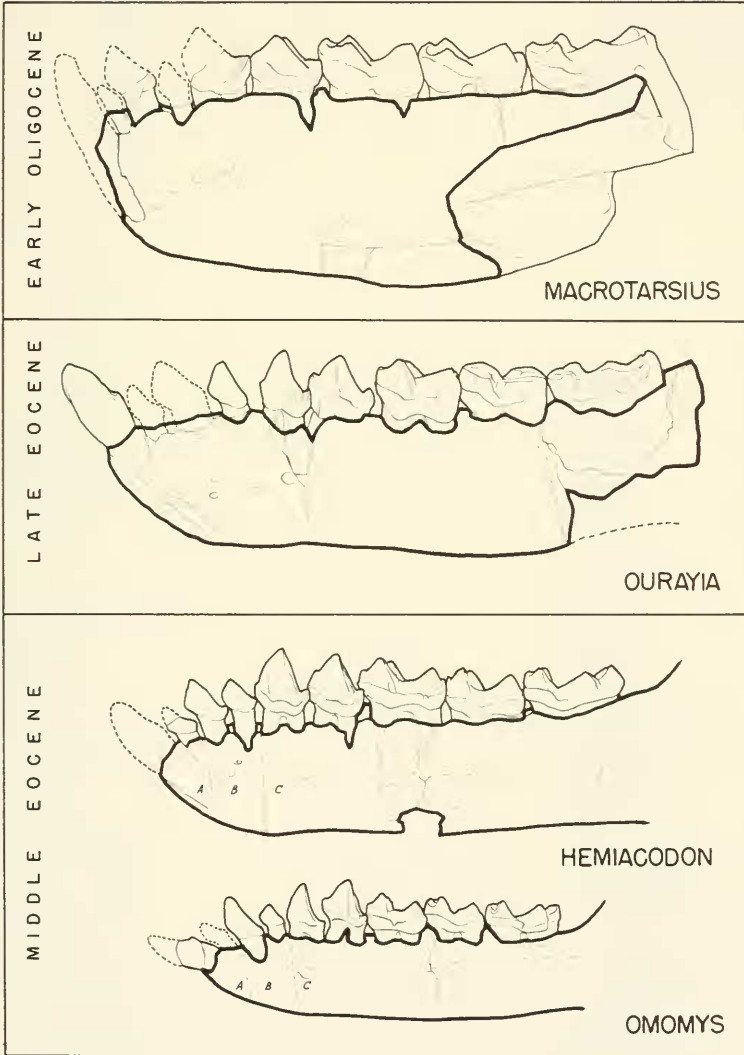


Figure 2.

Occlusal views of right upper, and left lower dentitions of *Ourayia uin-*
tensis, P.U. 16431, (M_1 reversed from right side), approx. x 5.5.

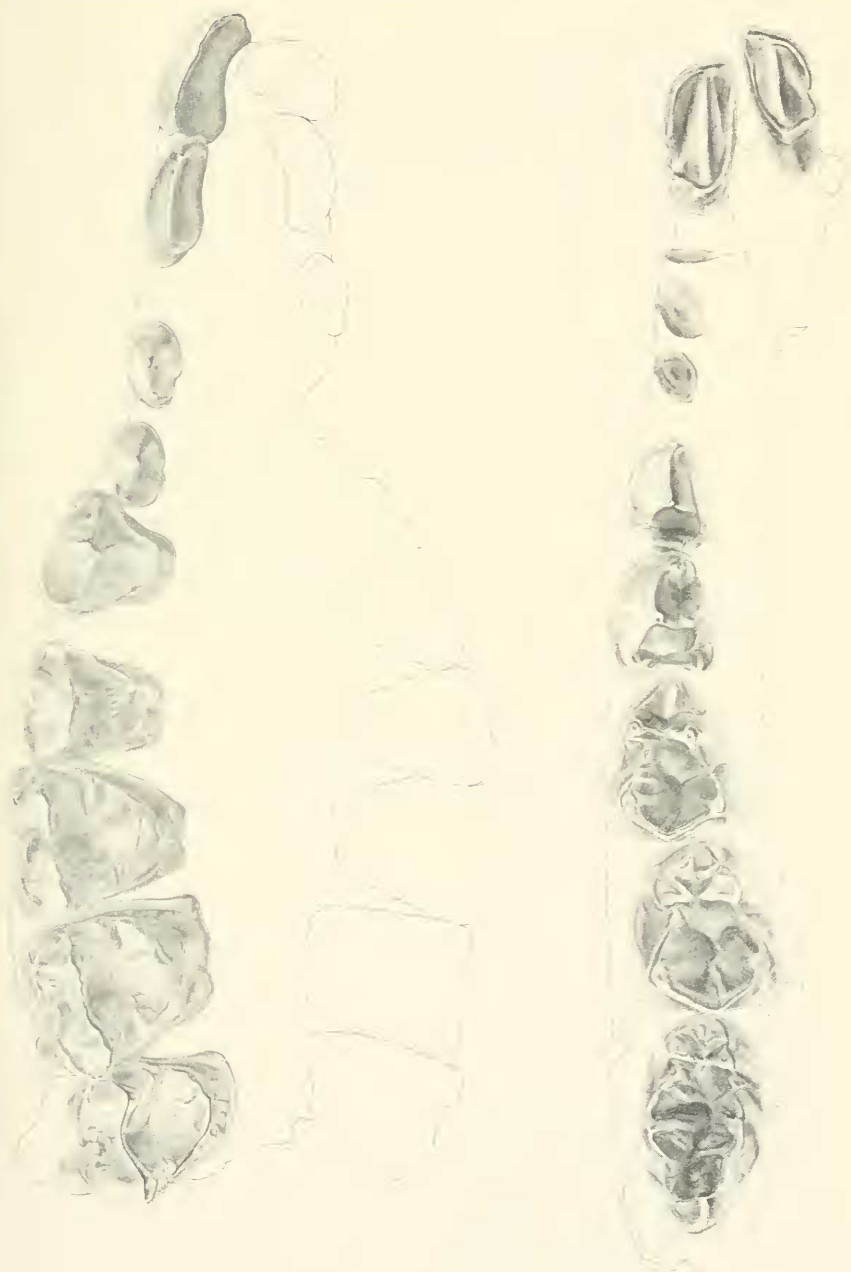


Figure 3.

Lateral view of right maxilla of *Ourayia uintensis*, P.U. 16431, approx.
x 5.5.



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